Sex-specific strategies in a sex-biased world

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CHAPTER 3

Does local competition affect sex-specific post-fledging juvenile survival in the great tit (*Parus major*)?

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Abstract

Competition between and within the sexes could affect the relative fitness benefits parents might gain from producing a certain offspring sex. Therefore, it is important to know if local population density and local population sex ratio shape sex-specific survival prospects of the offspring. We aimed at testing this by creating areas that varied in levels of sex-specific competition experienced by juveniles after fledging. Therefore, we simultaneously manipulated offspring sex ratios and densities on a local scale (plots). We observed colour-ringed juvenile great tits over a five-month period after fledging in two different years to estimate juvenile apparent survival probabilities in relation to the plot treatment. Our expectations were that high plot densities and male biased plot sex ratios would reduce male survival via intra-sexual competition for territorial space and female survival via inter-sexual competition for food. We show that in 2005, overall apparent post-fledging survival was 1.6 times higher in female compared to male biased plots, whereas in 2006 it was 2.4 times higher in male-compared to female biased plots. The original plot density seemed to affect apparent survival slightly negatively but the change in plot density did not relate to apparent survival. The effects of altered sex ratio and density were not different for male and female offspring. However, male and female fledglings differed in how their apparent survival varied over time with females having lower apparent survival in later months. The low survival of fledglings from female biased plots in 2006 was unexpected and might be due to reduced local survival or increased emigration from these plots. A possible explanation is that in 2006 the proportion of second broods produced was higher than in 2005. Parents could have traded off care to the first brood against care to the second brood in this year depending on the plot sex ratio. Our results provide experimental evidence that local offspring sex ratio does affect apparent juvenile post-fledging survival but that ecological conditions that differ between years shape the direction of this effect. The experimental manipulation probably triggered a cascade of reactions involving sex-specific post-fledging movements that lessened sex-specific effects on local survival.

Introduction

The optimal sex ratio produced by individuals is determined by the costs and benefits of producing a certain offspring sex under the prevailing circumstances. In this context survival until first reproduction of the offspring is a key fitness-component as it is one of the major sources of individual variation in lifetime reproductive success (Clutton-Brock, 1988; Newton, 1989).

Studies examining factors that affect sex-specific offspring survival during parental dependency are numerous and mainly investigated effects of individual parental traits (Kilner, 1998; Nager *et al.*, 2000; Rutkowska & Cichon, 2006; Rowland *et al.*, 2007), brood composition (Oddie, 2000; Råberg *et al.*, 2005; Müller *et al.*, 2007; Nicolaus *et al.*, 2009), hatching sequence (Torres & Drummond, 1997) or individual offspring traits (Slagsvold *et al.*, 1986; Kalmbach *et al.*, 2005; Vergara & Fargallo, 2008). Some studies also investigated variables that shape sex-specific survival after independence (Merilä *et al.*, 1997; Heeb *et al.*, 1999; Badyaev *et al.*, 2002; Potti *et al.*, 2002; Laaksonen *et al.*, 2004b; Husby *et al.*, 2006) and they found that survival of sons and daughter was differentially affected by hatching date (Husby *et al.*, 2006), position in the laying order (Badyaev *et al.*, 2002), body size (Merilä *et al.*, 1997) or ectoparasite infestation (Heeb *et al.*, 1999).

One aspect that has been mostly neglected is that the social environment is very likely to change sex-specific offspring survival and recruitment prospects. In many species we can expect frequency dependent selection in the form of intra- and inter-sexual competition to act on juveniles. In this context, local density and local sex ratio are two candidate traits that might affect the level of sex-specific competition experienced by individuals. The direction in which sex-specific competition can shape offspring survival prospects depends on a number of factors. First, in most bird species females show larger natal dispersal distances, as males presumably benefit relatively more from familiarity with the natal habitat for establishment of a territory (Greenwood, 1980; Greenwood & Harvey, 1982). Therefore higher local densities and especially higher local numbers of male offspring would relate to higher local competition for territories among males. Second, in sexually dimorphic species males tend to dominate females in competition for resources outside the breeding season such as food (Kluyver, 1951; Benkman, 1997; Tarvin & Woolfenden, 1997; Donald *et al.*, 2007) or winter roosting places (Kluyver, 1957; Feare *et al.*, 1995). Under increased local competition for a certain resource females would therefore be expected to perform less well. Third, it is necessary to know the spatial and temporal pattern at which competitive interactions take place. As shown by Brouwer *et al.* (2006) and Both and Visser (2000), density on the population level might not affect survival while on a smaller scale survival was negatively related to the number of group members in a territory (Brouwer *et al.*, 2006) or positively affected by territory size (Both & Visser, 2000). In most bird species during the breeding season the sexes need to cooperate to successfully raise offspring (Krebs & Davies, 1993), however competition between the

sexes can be more pronounced outside the breeding season when competition is mainly for resources such as food or roosting places (Newton, 1998).

To our knowledge there are so far no experimental studies in birds or mammals that investigated the consequences of competition between and within the offspring sexes for sex-specific survival prospects. The great tit (*Parus major*) is a good model system to test for effects of sex-specific competition for the following reasons. In our population tits are generally non-migratory and therefore competition on a local population scale can occur all year round. Additionally, natal dispersal distances are larger for female great tits (Greenwood *et al.*, 1979; Tinbergen, 2005). Furthermore, outside the breeding season there is scope for intense sex-specific competition. In flocks, competitive interactions can be observed within each sex and between the sexes (Drent, 1983). In competition for artificial food outside the breeding season males are generally dominant over females (Kluyver, 1957; Drent, 1983; Wilson, 1992). Juvenile males are subdominant to adult females before moult but they can become dominant thereafter (Drent, 1983). Post-fledging survival studies in the great tit have shown that especially in the first period after fledging juveniles suffer higher mortality rates (Dhondt, 1979; Drent, 1984; Naef-Daenzer *et al.*, 2001). In this period juveniles gain independence and have to start self-feeding. Additionally, between June and August juveniles start to show aggressive interactions more often (Hinde, 1952) and juvenile males start to establish a territory in autumn (Kluyver, 1951; Drent, 1983). Therefore, the period from fledging till October seems to be especially suitable to investigate sex-specific effects of intra- and inter-sexual competition on juvenile survival.

In a large-scale experiment, we simultaneously manipulated local population sex ratios and densities of great tit offspring during the nestling phase on a plot scale. We aimed at creating plots that varied in levels of sex-specific competition that birds experienced after fledging. We collected observations of colour-ringed juveniles over a five-month period in 2005 and 2006. Using individual resighting histories in the program MARK we explored whether there were sex-specific effects of the experimental plot treatments on juvenile survival and resighting probability. We expected that a high density and a male biased plot sex ratio would lead to increased levels of competition where juvenile females suffer from between sex competition and juvenile males from within sex competition. Thus survival of young that had fledged in such environments is expected to be reduced.

Methods

Study area

The study was conducted in the Lauwersmeer area which is situated in the north-east of the Netherlands (53°23' N, 6°14' E). In February 2005 we extended the existing study area by establishing 12 nest box plots where in some woodlots already existing

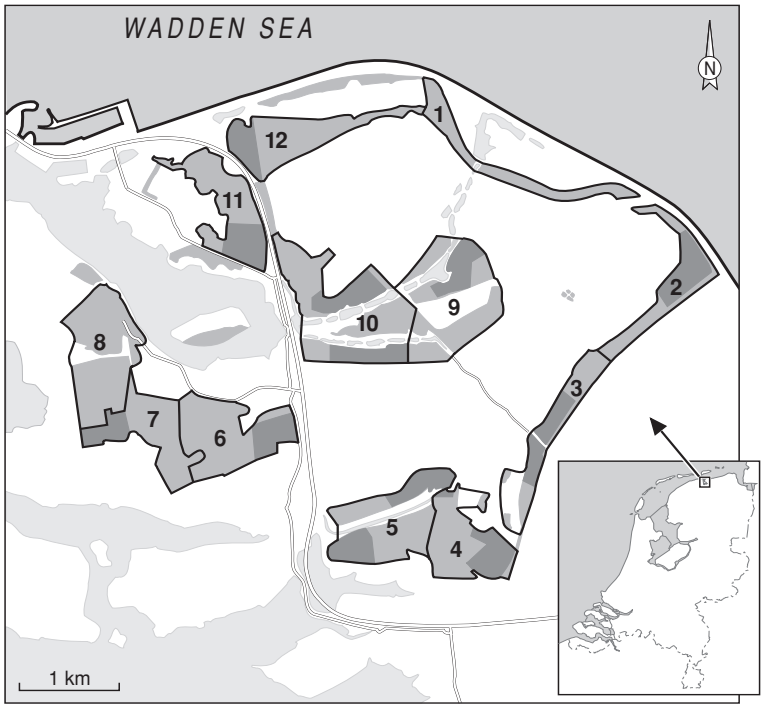

Figure 3.1 Map of the study area in the Lauwersmeer (53°23'N, 06°14'E), NL. The dark grey areas represent the 12 nest box plots and the numbered black-bordered areas are the 12 observation plots. Water is indicated in light grey, woodlots in medium grey, and open grass or agricultural areas in white.

boxes were rearranged in others they were newly put up (fig. 3.1). Each plot consisted of 50 nest boxes in a regular 50 m grid. The woodlots were primarily deciduous forests (about 30 year old plantations of oak (*Quercus robur*), poplar species (*Populus* spec.), birch (*Betula pubescens*), maple (*Acer platanoides*), ash (*Fraxinus excelsior*) and elder (*Alnus glutinosa*) and were separated by at least 300 m open grassland or forest patches without boxes.

Experimental design

We manipulated plot density and sex ratio (proportion of males) of nestling great tits in 2005 and 2006. Plot sex ratio treatments were either male biased, female biased or control (balanced sex ratio) and the plot density treatments were high or low density. We created six different combinations of sex ratio and density treatments ranging from male biased-low density to female biased-high density plots (fig. 3.2). Each treatment-combination occurred in two replicates per year and was semi-randomly allocated to plots each year (not allowing for a plot to have the same combination in consecutive years). To achieve the plot treatments, first broods (broods that started less than 30

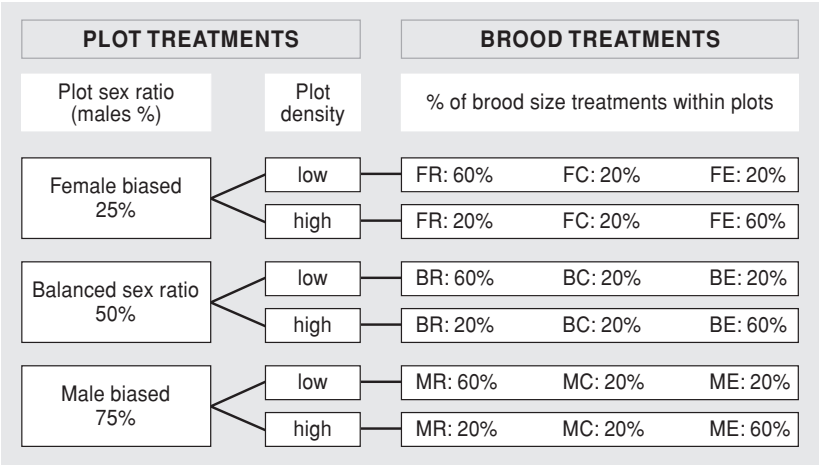

Figure 3.2 Experimental treatments applied to plots during the two years 2005 and 2006 combining sex ratio and density of juvenile great tits. The treatment at the plot level (sex ratio bias and low or high density) was achieved by manipulated 60% of the broods within a plot towards the desired treatment keeping 40% of the nests as controls for the other treatments. Sex ratio treatment for all broods within a plot was in the direction of the plot treatment. F: female biased brood, B: balanced/control sex ratio brood, M: male biased brood; R: reduced brood size, C: control brood size, E: enlarged brood size.

days after the start of the very first brood in that year) within plots were manipulated at day 6 after hatching. For the sex ratio manipulation all broods within a plot were manipulated in the direction of the plot treatment. The density manipulation was done by manipulating the majority of brood within plots in the desired direction (e.g. enlarging 60% of the broods within a plot increased the total number of nestlings per plot, fig. 3.2). Further details on the experimental manipulation are given in Nicolaus *et al.* (2009). Averages per plot for the treatment categories are given in table 3.1. Second broods and replacement broods of known first broods after failure were not manipulated.

Field methods

From the beginning of April nest boxes were checked weekly to establish the start of egg laying (back calculated assuming one eggs was laid per day) and the clutch size was determined at the onset of incubation. Before the expected hatching date nest boxes were checked daily to determine hatching date (day 0). We sampled a small quantity of blood (ca 5–10 µl) from the tarsal vein of all nestlings when they were two days old and clipped the end of their toe nails in a unique combination for later identification. Between day 3 and 5 molecular sex determination was performed such that on day 6 after hatching the sexes of all nestlings were known to allow accurate sex ratio manipulation of the broods. DNA was extracted using the Chelex method

Table 3.1 Overview of average natural (top in cell) and experimental (bottom in cell) values per treatment group for plot sex ratio (proportion of male juveniles) and plot density (number of young) in 2005 and 2006 in a Dutch great tit population.

	2005		2006	
Treatment group	mean±SD	n	mean±SD	n
Female biased plot sex ratio	0.49 ±0.02 0.24 ±0.005	4	0.47 ±0.06 0.24 ±0.02	4
Control plot sex ratio	0.47 ±0.02 0.49 ±0.008	4	0.50 ±0.02 0.49 ±0.01	4
Male biased plot sex ratio	0.50 ±0.03 0.74 ±0.019	4	0.49 ±0.04 0.79 ±0.03	4
Low plot density	156.83 ±28.27 137.83 ±26.35	6	134.33 ±48.73 119.67 ±48.90	6
High plot density	161.50 ±16.28 181.16 ±17.32	6	118.00 ±27.62 132.67 ±32.67	6

described by Walsh *et al.* (1991). Sex of the young was determined following Griffiths *et al.* (1998). The PCR products were separated by electrophoresis on a 2% agarose gel. On day 6 broods were manipulated and nestlings also received a numbered aluminium ring. At day 14 after hatching all nestlings were additionally provided with 3 colour rings in a unique combination with the aluminium ring. Nestlings leave the nest approximately 20 days after hatching, thus we performed nest box checks every second day from day 19 onward to determine fledging success.

Observations

One week after the earliest first broods had fledged in 2005 and 2006 we started observations to cover most of the forested part of the study area. The forested area was divided in 12 parts of about 30–50 ha each (fig. 3.1) and in every part we spent four hours per occasion to observe individual great tits and read their colour rings. Observations followed a regular schedule with biweekly observation occasions in June, July, August, September and October. To reduce observer effects, observers switched plots between occasions. Often plots were also shared between two observers at a given occasion.

Survival analysis

Survival and resighting probabilities of juveniles were analysed using Cormack-Jolly-Seber models (Lebreton *et al.*, 1992) in program MARK (White & Burnham, 1999) with the logit as default link function. We constructed individual resighting histories for marked first brood juveniles that were known to have fledged in 2005 (n = 1599) and 2006 (n = 1092). Fledging of the very first brood in 2005 was on the 25th of May and in 2006 on the 29th of May and the last first broods fledged on the 27th of June in

2005 and the 19th of June in 2006. The marked young entered the data as two cohorts (see below), the first cohort comprised all young that fledged within 12 days of the very first brood (2005: n = 1230, 2006: n = 907) and the second cohort comprised young that fledged within the following 12 days (2005: n = 369, 2006: n = 185). Differences between these cohorts were considered to be minor and therefore we assumed that they had the same probabilities of survival and resighting. We created seven resighting occasions. For the first cohort we had two 12-day observation intervals in June, for the second cohort we had one 12-day observation interval in June and for both cohorts we grouped biweekly observations in July-October into monthly observation intervals (interval length was adjusted in program Mark accordingly). In the observation matrix, individuals were scored as being seen alive at the first occasion following their fledging (when they entered the resighting history) and they were scored as being seen or not at each subsequent occasion. In the past, several studies on great tits showed that post-fledging survival (Naef-Daenzer *et al.*, 2001) and recruitment (Verboven & Visser, 1998; Monros *et al.*, 2002) of an individual young does not depend on the survival of its brood mates. Thus, we considered survival probability of fledglings from the same brood as independent from each other. The experimental plot manipulation was specifically effective in changing the plot sex ratio composition so that the original plot sex ratios were unrelated to the sex ratios after manipulation ($r_c = 0.21$, n = 24, $p > 0.05$), we therefore investigated the plot sex ratio treatment as fixed categorical effect. The experimental plot density was still related to the original density of young in a given plot ($r_c = 0.86$, n = 24, $p < 0.05$). We therefore used the original plot density of young and the experimental change in density of young per plot as continuous covariates.

We used Akaike's information criterion corrected for the sample size (AICc) to select the most parsimonious model (Akaike, 1973). Normalized Akaike weights were calculated to assess the relative likelihood of competing models. We investigated goodness-of-fit using median ĉ approach on the model including all two-way interactions between fixed effects which gave some indication for overdispersion ($\hat{c} = 1.74 \pm 0.03$ SE). AIC_c-values were adjusted for c-hat to account for the amount of overdispersion resulting in QAIC values.

We started the analysis with a global model (table 3.2, model 15) including the fixed effects: sex, plot sex ratio treatment, year and time and all two-way interactions for survival and resighting probability (3-way interactions were also tested but never had much support and are therefore not further mentioned to reduce complexity of the manuscript). Time represented the occasions for resighting (fledging of first cohort = occasion 1, 12 days after fledging of first cohort = occasion 2, 12 days after fledging of second cohort = occasion 3 (= end of June), end of July (occasion 4), end of August (occasion 5), end of September (occasion 6) and end of October (occasion 7)) and time represented intervals for survival (occasion 1 - 2, occasion 2 - 3, occasion 3 -July, July - August, August - September, September - October). Subsequently, we first constrained the resighting probabilities and then survival probabilities. The most

parsimonious model from this procedure was used to investigate a set of candidate models considering effects of the covariates original plot density and experimental change in plot density (Δ density) and their interactions with offspring sex, the plot sex ratio treatment, year and time. As the plot manipulation was carried out by manipulating broods, some variance of the plot density and sex ratio manipulation might originate from brood effects. To test this we included the brood covariates change in brood sex ratio (Δsr = sr before – sr after manipulation on days 6) and change in brood size (Δbs = bs before – bs after manipulation on day 6) for models that supported experimental plot variables. The effects of the brood treatment on survival were not further analysed in this study because current CMR-analysis cannot deal with such interdependencies between the brood and plot treatments as were caused by our experimental set-up. Including fledging weight as a covariate may partly correct for effects of the brood treatment. However, as the offspring sexes significantly differed in fledging weight (Nicolaus *et al.*, 2009) correcting for weight might mask sex-specific effects and might also mask effects of the experimental plot treatment. Therefore we choose not to include weight in our models. We thus only tested whether adding or removing experimental brood variables would change the significance of plot variables. This was done first separately for resighting probability and survival probability. Plot covariates that were significant for resighting probability were then also tested in the model with covariates for survival.

For the best model without covariates (table 3.2, model 1), estimates of apparent survival over the last interval (October) differed considerably between the years with a very low survival in 2005 (0.185 ±0.05 SE) and very high survival in 2006 (1.00 ± 0.001 SE). We consider these two estimates less trustworthy for the following reasons: First, the resighting probability for the last interval in 2005 was probably not estimable (estimate of 1 with a large associated standard error of 0.18) due to a rather low sample size (average of 9 individuals seen per plot vs. 20 in the interval before) and second the resighting probability for the last interval in 2006 was very small (0.06 ±0.01). We will thus not further discuss results from the last interval or occasion.

Results

Effects of sex, month, year and sex ratio treatment

SURVIVAL PROBABILITY

From the global model, the best supported model contained an effect of the plot sex ratio treatment on apparent survival that varied between years (table 3.2, model 1 vs. model 5, fig. 3.3). In 2005 over the entire period June-September, survival was lower for male biased (0.14) than for control (0.19) and female biased plots (0.23). In contrast, in 2006 overall survival was lower for female biased plots (0.14) than for control (0.24) and male biased plots (0.35, fig. 3.3). The years also differed in how apparent survival changed with time (table 3.2, model 1 vs. model 3, fig. 3.4). In 2005

the estimated survival probability was on average low in June (mean ±SE, survival over first interval: 0.60 ±0.05; survival over the second interval: 0.48 ±0.09) then increased in July (0.94 ±0.08), decreased in August (0.81 ±0.06) and then increased again September (0.997 ±0.14). In 2006 the survival probability was on average low over the first interval in June (0.44 ±0.06) but increased already over the second interval in June (0.75 ±0.12) to increased continuously until September (July: 0.85 ±0.06; August: 1.00 ±0.001; September: 0.99 ±0.20). There was no sex-specific effect of the plot sex ratio treatment on our estimates of apparent survival (table 3.2, model 4 vs. model 2). The two offspring sexes however differed in how apparent

Table 3.2 Summary of the model selection statistics from the global model starting set examining apparent survival (Φ) and resighting (P) probability of juvenile great tits in relation to effects of sex (s), plot sex ratio treatment (m), year (y) and time (t).

No.	Model	No. par	$QAIC_c$	$\Delta QAIC_c$	Quasi deviance	QAICc weights
1	Φ(s*t+m*y+y*t) P(y*t)	32	7755.46	0.00	7691.06	0.450
2	Φ(s*y+s*t+m*y+y*t) P(y*t)	33	7756.11	0.65	7689.68	0.325
3	Φ(s*t+m*y) P(y*t)	28	7757.85	2.39	7701.54	0.136
4	Φ(s*m+s*y+s*t+m*y+y*t) P(y*t)	35	7758.74	3.28	7688.26	0.087
5	Φ(m+s*t+y*t) P(y*t)	30	7766.97	11.51	7706.62	0.001
6	Φ(s+m*y+y*t) P(y*t)	27	7770.93	15.47	7716.64	0.000
7	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(m+y*t)	47	7773.01	17.55	7678.15	0.000
8	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(y*t)	45	7773.49	18.03	7682.70	0.000
9	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(m+s+y*t)	48	7774.74	19.28	7677.84	0.000
10	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(m+s*y+y*t)	49	7775.70	20.24	7676.76	0.000
11	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(s*y+m*y+y*t)	51	7779.33	23.87	7676.32	0.000
12	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(s*m+s*y+m*y+y*t)	53	7781.05	25.59	7673.96	0.000
13	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(s*m+s*y+s*t+m*y+y*t)	57	7782.39	26.93	7667.13	0.000
14	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(s*m+s*y+m*y)	49	7789.18	33.72	7690.24	0.000
15	Φ(s*m+s*y+s*t+m*y+y*t+m*t) P(s*m+s*y+s*t+m*y+y*t+m*t)	65	7790.04	34.58	7658.39	0.000

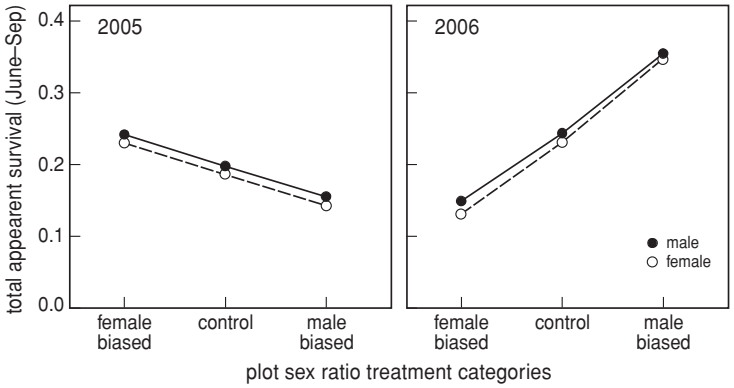

Figure 3.3 Total post-fledging survival until the end of September in relation to the plot sex ratio treatment in 2005 and 2006 for male and female young. Total survival estimates were obtained by multiplying real parameter survival estimates for the first five intervals.

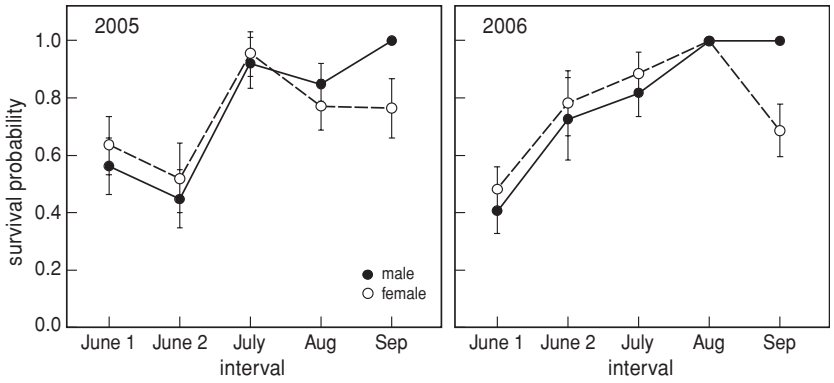

Figure 3.4 Apparent survival probabilities (±SE) over the first five intervals in 2005 and 2006 for male and female fledgling great tits from control plots. Real parameter estimates and standard errors are derived from the best model of the global model starting set (table 3.2, model 1).

survival varied with time (table 3.2, model 1 vs. model 6, fig. 3.4). Averaged over both years and the three treatment groups male apparent survival was low over the first two intervals in June (0.48 ±0.05 SE, 0.59 ±0.10 SE) and then increased to high levels in July (0.88 ±0.07 SE), August (0.996 ±0.06 SE) and September (1.00 ± 0.004 SE). Female survival probability was also low in June (0.56 ±0.07 SE and 0.66 ±0.10 SE) but high in July (0.93 ±0.07 SE), and August (0.99 ±0.10 SE) but decreased again in September (0.73 ±0.07 SE). Our main result is thus that the sex-ratio treatment did affect post-fledging survival, but that the effects were not specific with regard to offspring sex.

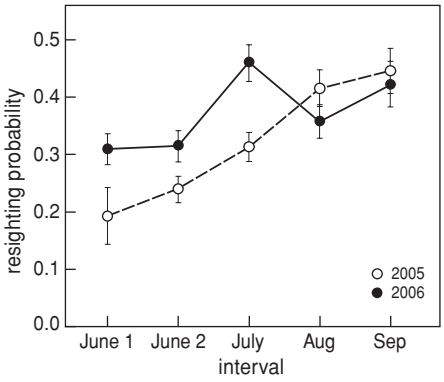

Figure 3.5 Juvenile resighting probabilities (±SE) over the first five occasions for the year 2005 and 2006. Real estimates and standard errors are from the best model from the global model starting set (table 3.2, model 1).

Resighting probability

Resighting probability showed a varying pattern with time that differed between years (table 3.2, model 12 vs. model 14, fig. 3.5). It varied between 0.2 and 0.4 for the first three occasions in 2005 and was about 0.4 in August and September. In 2006 it was about 0.3 for the two occasions in June and was close to 0.5 in July but slightly lower again in August and September (fig. 3.5). The data did not show much support for a model where resighting probability dependent on the plot sex ratio treatment (table 3.2, model 7 vs. model 8) or on sex (model 9 vs. model 7). There was no indication that resighting probability of the two sexes varied depending on the plot sex ratio treatment (model 14 vs. model 10).

Observed numbers

To show that the year specific effects of the plot sex ratio treatment were unlikely caused by single plot effects we inspected per plot the proportion of fledglings that was seen in the post-fledging period for the three plot sex ratio treatment categories and the two study years (fig. 3.6). If plot effects were responsible for the patterns found we would expect single lines in fig. 3.6 to lay outside the confidence intervals and pull the pattern for a given sex-ratio treatment groups. However, all plot within a given sex ratio treatment group in a year generally showed similar trends in the proportion of fledglings observed (fig. 3.6). In 2005 most plot-lines followed the average quite closely, not clearly supporting the estimated effect of the plot sex ratio treatment on apparent survival. In 2006, plots with a female biased sex ratio had generally a lower proportion of fledglings observed than male biased plots for both cohorts, giving good support to the observed apparent survival effect of the plot sex ratio treatment in this year (fig. 3.6).

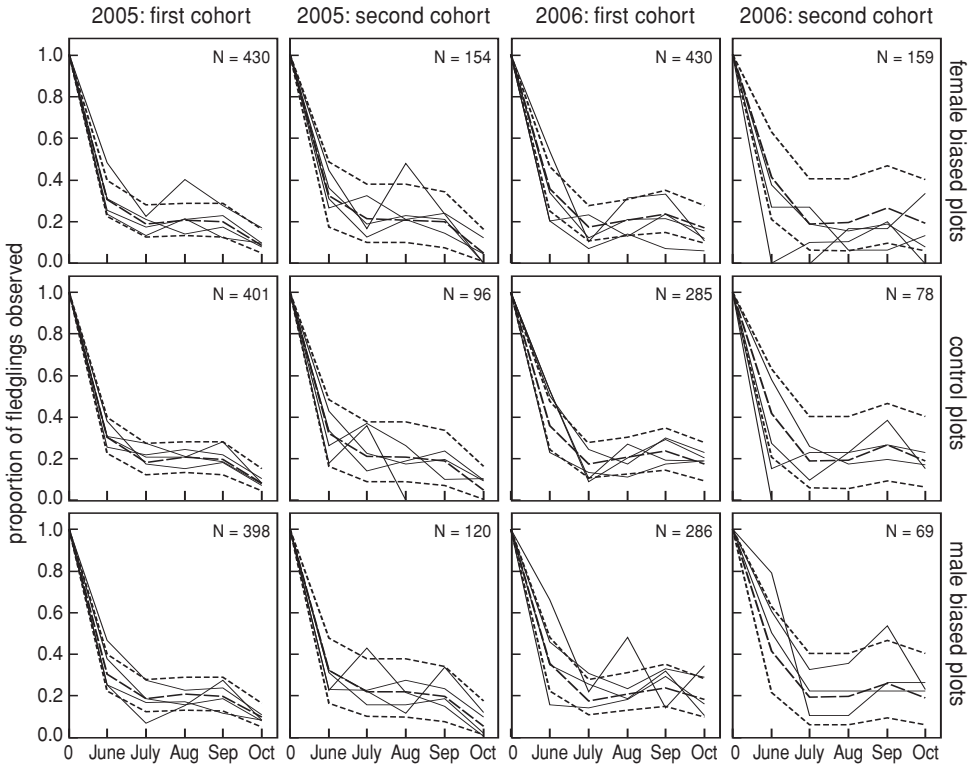

Figure 3.6 Proportion of fledglings observed per month in the post-fledging period starting from 100% at fledging (0 on x-axis). Single graphs elements show separate patterns for juveniles that fledged in the first 12 days (first cohort) and the following 12 days (second cohort) after the very first brood in 2005 and 2006 and for the three plot sex ratio treatment categories. Sample sizes of number of first and second cohort fledglings are indicated within plots. Each solid line represents the proportion of fledglings from a single plot that was seen again per month until October. Dashed lines indicates the average proportion of fledglings observed over all plots in a year from a given fledging-cohort and the dotted lines give the 95% asymmetric confidence interval around this average.

Density effects

RESIGHTING PROBABILITY

The resighting probability was negatively associated with the original plot density (oD effect in table 3.3, model 6 vs. model 17: $\beta = -0.006 \pm 0.001$ SE in model 3) and was negatively affected by the experimental change in plot density (ΔD effect in table 3.3, model 5 vs. 6: $\beta = -0.004 \pm 0.002$ SE in model 3) when correcting for original plot density. However, the effect of ΔD was not supported anymore when we included the effect of the brood size manipulation (on the nest level) in the model (Δbs in model 2: $\beta = -0.054 \pm 0.014$ SE, table 3.3, model 2 vs. model 3), which was the manipulation used to create the changes in density. The interaction between the plot sex ratio

Table 3.3 Model summary statistics examining *resighting probability* of juvenile great tits in relation to effects of original plot density (oD) and experimental change in plot density (ΔD). Basic model: Φ(s*t+m*y+y*t)P(t*y) is indicated as Φ(base)P(t*y). (s) = sex, (m) = plot sex ratio treatment, (y) = year, (t) = time and (Δbs) = change in brood size.

No.	Model	No. par	$QAIC_c$	$\Delta QAIC_c$	Quasi deviance	QAICc weights
1	Φ(base) P(y*t+m+oD+m*ΔD+Δbs)	39	7725.13	0.00	7646.54	0.425
2	Φ(base) P(y*t+oD+Δbs)	34	7725.46	0.33	7657.00	0.361
3	Φ(base) P(y*t+oD+ΔD+Δbs)	35	7726.70	1.57	7656.22	0.194
4	Φ(base) P(y*t+m+oD+m*ΔD)	38	7732.14	7.01	7040.79	0.013
5	Φ(base) P(y*t+oD+ΔD)	34	7734.28	9.15	7655.58	0.004
6	Φ(base) P(y*t+oD)	33	7737.53	12.40	7671.11	0.001
7	Φ(base) P(y*t+oD+t*oD)	38	7737.60	12.47	7661.04	0.001
8	Φ(base) P(y*t+s+oD+y*oD)	34	7738.66	13.53	7670.21	0.000
9	Φ(base) P(y*t+s+oD+s*oD)	35	7741.49	16.36	7671.01	0.000
10	Φ(base) P(y*t+m+oD+m*oD)	37	7742.71	17.58	7668.17	0.000
11	Φ(base) P(y*t+Δbs)	33	7747.16	22.03	7680.73	0.000
12	Φ(base) P(y*t+m+ΔD+m*ΔD)	37	7749.52	24.39	7674.98	0.000
13	Φ(base) P(y*t+ΔD+y*ΔD)	34	7754.63	29.50	7686.17	0.000
14	Φ(base) P(y*t+s+m+oD+s*m+m*oD+s*oD +s*m*oD)	43	7754.67	29.54	7667.95	0.000
15	Φ(base) P(y*t+s+ΔD+s*ΔD)	35	7755.14	30.01	7684.66	0.000
16	Φ(base) P(y*t+ΔD)	33	7755.26	30.13	7688.83	0.000
17	Φ(base) P(y*t)	32	7755.46	30.33	7691.06.	0.000
18	Φ(base) P(y*t+ΔD+t*ΔD)	38	7757.13	32.00	7680.57	0.000
19	Φ(base) P(y*t+s+m+ΔD+s*m+m*ΔD+s*ΔD +s*m*ΔD)	43	7758.94	33.81	7672.22	0.000

treatment and Δ density received some support when not controlling for Δbs (table 3.3, model 4 vs. 5) but lost support when we controlled for Δbs (table 3.3, model 1 vs. 2). The original density did not interact with the sex ratio treatment to affect resighting probability (table 3.3, model 10 vs. 6). There was no evidence that original or Δ density sex-specifically affected resighting (table 3.3, model 9 and 15). The data did not support a sex-specific interaction effect between experimental plot sex ratio and Δ density or original density (table 3.3, model 14 and 19). Original density and Δ density did not vary with year or time to affect resighting (table 3.3, oD: model 8 and 7; ΔD: model 13 and 18).

So the main findings are that resighting probability was lower in plots with a higher natural density of fledglings and for nests with experimentally increased brood size. The density before and after manipulation per plot was still strongly correlated, thus plots with high original densities also had high final densities of fledglings. Higher densities could have increased the mobility of flocks (Chen & Hsieh, 2002) which left less time for the detection of complete ring combinations. However, a sort of dilution effect could have also made the identification of individuals at higher densities more difficult.

Survival probability

The survival probability was negatively associated with the original density (table 3.4, model 8 vs. 17, oD: $\beta = -0.006 \pm 0.002$ SE). Again a negative effect of ΔD (table 3.4, model 9 vs. 17, ΔD: $\beta = -0.007 \pm 0.003$ SE) lost support when we included the strong negative effect of Δbs in the model (table 3.4, Δbs in model 3: $\beta = -0.080 \pm 0.023$ SE, model 3 vs. model 4).

Modelling oD and Δbs for both resighting and survival simultaneously revealed that the original density did not further improve survival when it was already fitted to resighting (table 3.4, model 2 vs. model 1) but when it was removed from resighting strongly decreased the model fit (table 3.4, model 2 vs. 4). The Δbs did not seem to affect resighting anymore when it was included in survival (table 3.4, model 5 vs. 6). This indicates that the original plot density mainly was important for the resighting probability while the brood size manipulation mainly affected survival.

The interaction sex ratio treatment * Δ density did not improve apparent survival (m*ΔD in table 3.4, model 10 vs. 9). The original density also did not interact with the sex ratio treatment to affect survival probability (m*oD in table 3.4, model 7 vs. 8). There was no evidence that original or Δ density sex-specifically affected survival (table 3.4, model 12 and 15). The data did not support a sex-specific interaction effect between experimental plot sex ratio and Δ density or original density for survival probability (table 3.4, model 18 and 19). Original plot density and Δ density did not vary with year or time to affect survival (table 3.4, oD: model 13 and 11; ΔD: model 14 and 16). Furthermore, the interaction between the covariate Δ brood sex ratio * year was considerably less well supported than the interaction plot sex ratio * year, suggesting that sex ratio was effective mainly on the plot and not on the brood level (Δsr in table 3.4, model 17 vs. 20).

Table 3.4 Model summary statistics examining *survival probability* of juvenile great tits in relation to effects of original plot density (oD) and experimental change in plot density (ΔD). Basic model: Φ(s*t+m*y+y*t)P(t*y) is indicated as Φ(base)P(base). (s) = sex, (m) = plot sex ratio treatment, (y) = year, (t) = time, (Δbs) = change in brood size and (Δsr) = change in brood sex ratio.

No.	Model	No. par	$QAIC_c$	$\Delta QAIC_c$	QAICc weights
1	Φ(base+Δbs) P(base+oD)	34	7720.62	0.00	0.350
2	Φ(base+oD+Δbs) P(base+oD)	35	7720.78	0.16	0.323
3	Φ(base+oD+ΔD+Δbs) P(base)	35	7730.46	9.84	0.003
4	Φ(base+oD+Δbs) P(base)	34	7730.63	10.01	0.002
5	Φ(base+Δbs) P(base+Δbs)	34	7738.99	18.37	0.000
6	Φ(base+Δbs) P(base)	33	7739.05	18.43	0.000
7	Φ(base+oD+m*oD) P(base)	35	7748.83	28.21	0.000
8	Φ(base+oD) P(base)	33	7748.96	28.34	0.000
9	Φ(base+ΔD) P(base)	33	7749.43	28.81	0.000
10	Φ(base+ΔD+m*ΔD) P(base)	35	7749.93	29.31	0.000
11	Φ(base+oD+t*oD) P(base)	38	7750.03	29.41	0.000
12	Φ(base+oD+s*oD) P(base)	34	7750.80	30.18	0.000
13	Φ(base+oD+y*oD) P(base)	34	7750.93	30.31	0.000
14	Φ(base+ΔD+y*ΔD) P(base)	34	7751.24	30.62	0.000
15	Φ(base+ΔD+s*ΔD) P(base)	34	7751.46	30.84	0.000
16	Φ(base+ΔD+t*ΔD) P(base)	38	7753.52	32.90	0.000
17	Φ(base) P(base)	32	7755.46	34.84	0.000
18	Φ(base+oD+s*m+s*oD+m*oD+s*m*oD) P(base)	40	7755.95	35.33	0.000
19	Φ(base+ΔD+s*m+s*ΔD+m*ΔD+s*m*ΔD) P(base)	40	7757.15	36.53	0.000
20	Φ(base+y*Δsr) P(base)	30	7760.55	39.93	0.000

Observed numbers and recruitment

If the patterns found for apparent post-fledging survival were due to real local survival effects and not temporary emigration from the study area we should find that: 1. the proportion of fledglings that recruited differed between the plot sex ratio categories in a similar way as for the apparent survival rates and 2. the proportion of recruited fledglings that was never observed in the post-fledging phase was equal between the plot sex ratio treatment categories. 3. differences between recruitment rates and post-fledging survival rates might be caused by differential survival after the post-fledging observation period.

There was rather strong qualitative support, that the year specific experimental plot sex ratio effects on apparent post-fledging survival were mirrored in the recruitment rates. For 2005, young from female biased plots recruited at a higher rate to the following breeding season than young from male biased plots (table 3.5). In 2006, the proportion of fledglings that recruited was significantly higher for male biased than female biased and control plots (table 3.5). In 2005, female biased plots had the highest proportion of recruits that was never observed in the post-fledging period, significantly higher than control plots, which may mean that we underestimated the higher post-fledging survival of young from female biased plots in that year, because

Table 3.5 Differences for 2005 and 2006 between the three plot sex ratio treatment categories for three different proportions of young: A) The proportion of fledglings that recruited to the next breeding season (number of recruits/number of fledglings). B) The proportion of recruits to the next breeding season that was never observed in the post-fledging observation phase (number of recruits never observed during post-fledging phase/total number of recruits). C) The proportion of young that was observed at least once in the post-fledging observation period and that recruited to the next breeding season (number of recruits seen during post-fledging phase/total number seen during post-fledging phase). Upper numbers in cells give the count of young and lower numbers give proportions. P-values were obtained from Fisher's exact test in a 2x2 contingency table.

	Female biased	Control	Male biased	F-C	F-M	C-M
A) Recruits from 05	53/584 0.09	39/497 0.08	33/518 0.06	P=0.512	P=0.011	P=0.393
Recruits from 06	58/370 0.16	60/367 0.16	82/355 0.23	P=0.841	P=0.014	P=0.025
B) Recruits 05 never seen	11/53 0.21	1/39 0.02	5/33 0.15	P=0.011	P=0.087	P=0.581
Recruits 06 never seen	11/58 0.19	11/60 0.18	13/82 0.16	P=1.00	P=0.654	P=0.821
C) Young seen and recruited 05	42/333 0.13	38/276 0.14	28/236 0.11	P=0.718	P=0.897	P=0.597
Young seen and recruited 06	47/192 0.24	49/230 0.21	69/241 0.29	P=0.485	P=0.382	P=0.071

young from these plots remained often undetected. In 2006, the proportion of fledglings that recruited but was not observed in the post-fledging period did not differ between the plot sex ratio treatment categories. However, in 2006 male biased plots tended to have a higher proportion of young seen in the post-fledging period that recruited in the next breeding season (table 3.5) than control and female biased plot. The lower apparent survival of young from female biased plots in 2006 might however still be caused by gradually occurring emigration from the study area.

Discussion

We found an effect of the plot sex ratio treatment on apparent juvenile post-fledging survival that differed strongly between years. In 2005 young from female biased plots survived 1.6 times better than young from male biased plots, whereas in 2006 young from male biased plots survived 2.4 times better than young from female biased plots. Interestingly, young from control plots showed intermediate apparent survival in both years. We are quite confident that these results were not confounded by single "plot effects" but represent actual treatment effects, as investigating the observed proportion of fledglings per plot over the post-fledging period showed similar patterns for the majority of plots in a given treatment group. We found no evidence for any sex-specific effect of the density or the plot sex ratio treatment on survival or resighting probability of juvenile great tits. However, the sexes differed in how their apparent survival changed in the course of the season with a decreasing apparent survival for females in the later months. Survival was also negatively affected by the experimental change in brood size which took over the variation from a negative effect of change in density. Therefore, negative effects of increased density were due to the fact that young from those plots mostly originated from broods that had obtained additional young. The negative effect of brood size enlargement on survival of young is not the topic of this paper and is thus discussed elsewhere (see Nicolaus *et al.* unpublished ms).

The main constraint of our study was that we cannot clearly exclude that effects on survival were caused by permanent emigration of individuals from the study area. Our study site is not directly connected to other forested areas but the next bigger village is 2.5 km away and the next bigger patch of forest (without nest boxes) is 2 km away. These are distances that have been reported to be travelled by individual great tits (Dhondt, 1979) and even entire families (Van de Casteele & Matthysen, 2006) in the post-fledging phase. Therefore, we will discuss the results found for apparent survival also for the possibility of gradually occurring emigration and we will discuss differences to results obtained from recruitment rates.

Experimental effects

Our expectations were that high local densities and a male biased plot sex ratio would lead to increased levels of competition and thus lower survival of male and female

young. The main experimental effects on post-fledging juvenile survival were of the plot sex ratio treatment, and in 2005 we found support for lower survival in male biased plots, but in 2006 the effect was opposite to our expectations. The experimental change in density did not seem to have any strong effects on either survival or resighting probability. This might be because the absolute numbers of young per plot that were added or removed were relatively small compared to the original densities of young and might have only changed the levels of competition experienced by juveniles to a small extent. Furthermore, we showed elsewhere that in the post-fledging period juveniles quickly redistributed themselves over the area such that especially for the density treatment the experimental plot bias was altered already in June (box A). The effect of the plot sex ratio treatment showed that competition did affect survival of juveniles as expected in 2005 while the opposing results from 2006 where rather unexpected. In 2006 a higher proportion of males did not relate to higher mortality, therefore more complex mechanisms seem to act on juvenile survival and we can only speculate how this pattern came about. In 2006 the proportion of second broods produced was considerably higher (32%) than in 2005 (9%). If parents in female biased plots would have reduced post-fledging care to their first broods more strongly than parents in control and male biased plots after initiating a second brood this might explain the patterns found. 2006 was a year with lower overall population size and therefore male broods might be valued relatively more than female broods as male young have a higher chance of getting a local territory at low densities (Kluyver, 1951; Van Balen, 1980; Drent, 1983). Parents in female biased plots might have traded-off care to the first brood against care to second brood young. That the initiation of a second brood reduces parental care to first brood young has been found in great tits (Verhulst & Hut, 1996) and in barn swallows (*Hirundo rustica*; Grüebler & Naef-Daenzer, 2008). However, whether the trade-off between investment in first brood fledglings and the second brood depends on the first brood's sex ratio or even the local sex ratio still remains to be established. Another explanation for the pattern in 2006 is the higher post-fledging movement of females (Dhondt, 1979; Drent, 1984) that might have created higher emigration rates of entire flocks from female biased plots. Dhondt (1979) showed that although dispersal distances within the forest did not differ between the sexes there were eminent differences in terms of emigration and immigration from forests between the sexes. We consider this explanation to be less likely though, because then apparent survival in the post-fledging phase should have been lower for female biased plots in both years. Furthermore, emigration should have occurred already quickly after fledging as we generally did not find stronger dispersal from female biased plots (chapter 4). Furthermore, as we did not find any survival difference between the sexes in response to the plot sex ratio treatment, emigration from plots should have occurred independently of juvenile sex.

The differences in apparent survival between the plot sex ratio treatment categories were generally reflected by the recruitment rates the next year. Recruitment rates of fledglings from 2005 showed a significant difference between the treatment

categories with higher recruitment from female biased plots than male biased plots. A higher proportion of fledglings from female biased plots in 2005 was never observed in the post-fledging period though still alive and was therefore assumed dead. This indicates that more individuals from female biased plots in 2005 had left the area quickly after fledging possibly still in the family phase. If they could have been detected, apparent post-fledging survival for female biased plots in this year might have been even higher. For 2006 the results for the recruitment rates scaled in the same direction as the pattern for post-fledging survival. Young from female biased plots had lower recruitment rates than young from male biased plots with control plots lying in between. Young from male biased plots seemed to survive at a higher proportion after the post-fledging observation period until the next breeding season which might explain their significantly higher recruitment rate compared to that of young from the other treatment groups. We need to note here that when we analysed recruitment rates with a three year data set (2005-2007) and in a more sophisticated model there was no significant overall effect of the plot sex ratio treatment (chapter 4) and the treatment effect did not vary significantly between years but the patterns for 2005 and 2006 scaled in the same direction as the results presented here (unpublished data).

An explanation for the lack of sex-specific treatment effects on apparent survival might be that juveniles showed sex-specific dispersal in response to plot sex ratio and high original local densities (see chapter 4). Males generally moved further from originally high density plots in the post-fledging period than females. Female young on the other hand increased their distances from male biased plots, especially in the later months when males start to become territorial, while males did not show this pattern (chapter 4). Furthermore, the experimental sex ratio bias of the plots was reduced continuously and had disappeared at latest in August 2005 and September 2006 due to movements between plots (box A). This is when males start to show territorial behaviour and competition between males is expected to increase. By moving to other areas individuals might have reduced the local competition experienced and thus could have influenced their own survival chances. Because males and females showed different dispersal strategies, this most likely obscured sex-specific effects of the plot sex-ratio treatment on survival.

Non experimental effects

Studies that investigated post-fledging survival rates in great tits found variable results with respect to when the highest mortality rates occurred. The study of Naef-Daenzer *et al.* (2001) showed highest daily mortality rates for fledglings in the first few days after leaving the nest. They also found that average daily mortality rates peaked in mid-June about five weeks after fledging of the earliest broods. The interpretation of these results was that there was seasonal variation in post-fledging survival where later fledged young had lower survival probabilities. Drent (1984) found highest weekly mortality rates of fledglings during mid to end of June. He called this phase

the critical period when most juveniles gain independence and have to start self-feeding. Our results seem to be in better agreement with the findings of the study of Naef-Daenzer *et al.* (2001). We found generally lower monthly survival rates during the first interval in June. The low survival over the second interval in 2005 might originate from lower survival rates of the second cohort of young and this is thus best explained by a negative effect of fledged date. That the same pattern was not observed in 2006 could be due to the fact that 2006 was a year with better food conditions later in the season, also supported by the higher proportion of second broods initiated in that year. However, differences in climatic variables or population density (higher in 2005) between years might also have caused this difference in the second interval.

While males and females had similar patterns of survival until the end of July in 2005 and end of August in 2006, differences became apparent thereafter. Males had high apparent survival in August and even 100% survival in September 2005 while that of females was noticeably lower and also in 2006 females had a lower apparent survival in September than males. We have some evidence that the lower apparent survival of females in later months is due to temporal emigration out of our study area. During roosting checks in December and January as well as during mist-net catches in autumn and winter more adult and juvenile males have been recorded whereas during nest box checks in February and March the number of females increased again (box D, but also see Kluyver (1957)).

Conclusions

Our study was not able to confirm or to refute that sex-specific competition among the offspring is important for survival of juvenile great tits. The experimental manipulation of the local number and sex ratio of juveniles probably triggered a series of processes including sex-specific dispersal in the post-fledging phase and the production of second broods (Nicolaus *et al.* unpublished ms). Strong movements already early after fledging, whether directed or random, could have added to the regulation of local numbers and sex ratios in the study area. The behaviour of families, flocks and single individuals as well as interactions with offspring from second broods might have contributed to the patterns we observed.

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